Group and kin recognition via olfactory cues in chimpanzees (*Pan troglodytes*)

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Abstract

Primates were traditionally thought to have a reduced sense of smell. Although there is now evidence that olfaction plays a greater role in primate social life than previously assumed, research on the sense of smell in non-human apes is scarce. Chimpanzees sniff the ground and vegetation on boundary patrols, but the function of this behaviour is unclear. Since chimpanzees are highly territorial and can kill individuals that do not belong to their own community, sniffing might function to gather information about conspecifics, particularly concerning group membership and kinship. To investigate whether chimpanzees recognize group members and kin via olfactory cues, we conducted behavioural bioassays on two groups of chimpanzees at Leipzig Zoo. In a pilot study, we found that chimpanzees responded more strongly to urine than to faeces or body odour. We then presented urine from group members, outgroup individuals and an unscented control in aerated boxes using a simultaneous discrimination task. The first behaviour after a chimpanzee first approached a box was related to olfaction (sniffing, nose within 20 cm, licking) in 83% of cases, highlighting the importance of olfaction as a general investigation mechanism in this species. Chimpanzees sniffed significantly longer at urine stimuli than the control and significantly longer at odours from outgroup individuals than those from group members. Furthermore, the duration of sniffing was positively correlated with relatedness. Our results suggest that chimpanzees use olfactory cues to obtain information about social relationships and fill a gap in our understanding of primate chemical communication.

Key Words

Olfaction, chimpanzees, chemical communication, bioassay, group recognition, kin recognition

Introduction

Olfaction is among the oldest senses [1] and influences social behaviour such as territorial defence, kin recognition and mate choice in many species [2,3]. In contrast to other mammals, research on olfaction in the primate order was neglected for decades, mostly because primates were considered to be "microsmatic" (having a poor sense of smell), relying more on visual and acoustic rather than olfactory cues [4,5]. The notion that primates are microsmatic was primarily based on anatomical evidence such as a reduction in the proportional size of the olfactory epithelium and olfactory bulb volume as compared to most other mammalian species [6,7] or a decrease in functional olfactory receptor genes [8,9]. However, neuroanatomical features are not necessarily correlated with olfactory performance [5].

Good olfactory capabilities are now recognized in some primate taxa, but not in others. Strepsirrhines (lemurs, lorises and galagos) and platyrrhines (New World monkeys) rely heavily on olfactory communication, showing classical scent marking behaviour and/or possessing specialized scent glands [10,11]. For example, callitrichids use olfactory cues to detect ovulation [12] and familiar individuals [13], and lemurs signal information including identity and relatedness in their glandular secretions which conspecifics can perceive in experiments [14–16]. In contrast to strepsirrhines and New World monkeys, catarrhines (Old World monkeys and apes, including humans) do not seem to have a functional vomeronasal organ (VNO) and accessory olfactory bulb (structures related to the perception of pheromones), at least postnatally [17]. However, the main olfactory system may also perceive social signals [18] and recent evidence suggests that social odorants serve a signalling function in Old World monkeys [e.g. 19–26]. Evidence for human chemo-signalling is also growing, indicating that olfaction may play a greater role in humans than previously assumed [27,28]. For example, humans have excellent odour discrimination abilities [29] and an unexpectedly high olfactory sensitivity that exceeds that of mice, rats and dogs for some substances [30]. Furthermore, humans may use chemosignals in mate choice [31,32] and can recognize kin via body odour alone [33–35].

Given the importance of olfaction in other primates including humans, the scarcity of research on the sense of smell in non-human great apes (hereafter apes) is surprising and leaves an important gap in our understanding of primate chemical communication. Although observations suggest that they use their sense of smell in various contexts [36], can discriminate between natural odors [37] and detect contaminants [38,39], no experimental investigations yet exist examining which social information apes perceive via odours. Human rater studies suggest, however, that gorillas (*Gorilla gorilla gorilla*) produce individually identifiable body odours [40] and that wild gorilla silverbacks use body odour as a flexible, context dependent signalling mechanism to group members and outgroup conspecifics [41].

Chimpanzees (*Pan troglodytes*) are one of our two closest living relatives and an important model species for understanding human evolution [42]. Wild chimpanzees sniff their environment while males sniff more frequently in sexual and social contexts and females more frequently in a feeding context [43]. Chimpanzees also often sniff the ground, vegetation and signs of chimpanzees such as nests, faeces and urine while patrolling the borders of their territory [44,45]. However, the function of sniffing behaviour during boundary patrols is unclear. Since chimpanzees live in multi-male, multi-female communities with high fission-fusion dynamics where community members may not meet for several days [46,47], and since chimpanzees are highly territorial and often kill individuals from other communities [44,48], obtaining information about the whereabouts of group members and outgroup individuals and the ability to discriminate between the latter are crucial for maximizing fitness, and it seems likely that they use olfaction to perceive this information.

In addition to recognizing group members, chimpanzees may maximize inclusive fitness through kin recognition, which is important to avoid inbreeding [49] and prevent infanticide [50]. Chimpanzees bias their behaviour towards and form strong social bonds with relatives [51–54, but see 55], and breed with genetically dissimilar mates [56], suggesting they can recognize their kin. Although they have excellent facial recognition abilities [57,58], olfactory cues may also be important for kin recognition in chimpanzees, given their fission-fusion behaviour and often dense habitat.

We report behavioural bioassays investigating the signalling function of social odours in apes. Our first aim was to test whether chimpanzees can distinguish between group members (ingroup individuals) and non-group members (outgroup individuals) using olfactory cues. In a simultaneous discrimination task, we presented two groups of zoo-living chimpanzees with urine from ingroup and outgroup individuals and an unscented control. If chimpanzees can discriminate between in- and outgroup urine, they should show a differential behavioural response towards the odour stimuli. We predicted that chimpanzees will investigate urine longer than the unscented control and outgroup urine longer than ingroup urine. Our second aim was to investigate whether chimpanzees can recognize their kin via olfactory cues. Since chimpanzees bias their behaviour towards relatives, we predicted that they will respond more strongly towards kin than non-kin odour.

Material and Methods

a. Study site and population

We studied two groups of captive chimpanzees (groups A and B) at the Wolfgang Köhler Primate Research Center at Leipzig Zoo from December 2015 to February 2016. At the time of the study, group A contained 18 (11 females, 7 males) and group B seven (6 females, 1 male) individuals. We excluded one male infant in group A since its behavioural responses were influenced by its mother. The subjects' age ranged 6-50 years (mean±SD=25±13 years, ESM 2 table S1). Each group

has access to spacious inside and outside enclosures with regular feeding, daily enrichment and water available *ad libitum*.

b. Pilot study on odour source preference

In a pilot study, we tested which odour source chimpanzees respond most strongly to by presenting three different odour sources (body odour, faeces and urine) from the same group member to both groups. Chimpanzees reacted most strongly towards urine, so we used urine as an odour source for subsequent bioassays. The increased inspection time of urine compared to faeces might reflect a trade-off between gathering information about the scent donor and infection risk from faeces (see electronic supplementary material (ESM) 1 for detailed methods, results and discussion).

c. Urine collection

We collected urine samples from adult chimpanzees in both groups at Leipzig Zoo using disposable pipettes directly after animals urinated on the floor in the sleeping or observation rooms and stored them in 15 ml plastic tubes at -20°C until use. We used new pipettes for each individual and only collected urine that we could assign to an individual. For females, we only collected urine when they showed no sexual swelling and were not menstruating, to avoid hormonal influences of the menstrual cycle on the odour.

d. Behavioural Bioassay

Ingroup vs. outgroup and olfactory sensitivity

To test whether chimpanzees can discriminate between ingroup and outgroup individuals via olfactory cues, we presented urine from one ingroup individual and one outgroup individual, and an unscented control (to test whether animals perceive urine over background) simultaneously 1 m apart in three plexiglass boxes (12 x 12 x 20 cm^3) installed on a metal grid on the ground in the inside enclosure (ESM 2 fig. S1). The odourless boxes were locked with padlocks, had multiple holes (3 mm in diameter) on each side and were lined with odourless wire mesh (mesh size: 0.5 mm) to prevent chimpanzees from using sticks to reach the contents. Thirty minutes prior to each session, we thawed samples and the experimenter (SH) rated their odour intensity on a scale of 0-10 to control for a potential influence of odour intensity on response behaviours. We placed 15 ml of each urine sample on a small piece of 100% cotton in the test boxes and a piece of cotton without urine in the control box. We always handled boxes with odourless disposable vinyl gloves to avoid transferring human body odour to the test apparatus.

We installed boxes in the morning before the chimpanzees entered the inside enclosure and removed them as soon as the animals left the enclosure (session duration 7h18m-8h33m, mean±SD = 8h8m±20m). All group members present in the inside enclosure could visit the boxes at any time, a more natural situation than testing subjects individually. Although this means that data for individual animals may depend on that of other animals, our observations did not suggest that this was the case. After each session, the experimenter assigned a new intensity score to each sample to assess changes in odour intensity over time. We disinfected boxes for an hour with a 4% solution of aldehyde-free antiseptic cleaner (OROsept K, Kleen Purgatis GmbH) then rinsed them thoroughly with water after each session.

We counterbalanced the location of the three stimuli (ingroup, outgroup, control) to control for potential side preferences. We used urine from 15 different individuals (10f, 5m) and conducted 6 sessions per group: 3 sessions with only female odours and 3 sessions with only male odours (we assigned sex order randomly). We conducted sessions at intervals of at least 6 days (range = 6-17 days, mean±SD = 8.9±3.8 days) to reduce habituation effects.

We recorded the chimpanzees' behavioural reactions towards the odour stimuli using a digital video camera (Panasonic HC-V757 HD), positioned on an observer platform outside the enclosure.

e. Video Analysis and Behavioural Definitions

SH analysed videos frame-by-frame using Mangold Interact version 16.1.0 (see ESM 3 for example video). We recorded the durations and time stamps of response behaviours. Our main target response behaviour was *sniffing* (defined as placing the nose within 3 cm of the box), but we also included the olfaction-related responses *nose within 20 cm* and *licking*, and the non-olfaction related responses *presence within 50 cm*, *touching* and *manipulating* (ESM 2 table S2). For analysis, we combined *touching* and *manipulating* into one response variable ('*manipulating'*) to measure tactile investigation of odours. To determine the mode of first investigation, we used the first behaviour shown when an animal first arrived at the boxes. To gain insight into whether chimpanzees perceive and discriminate odours from more than 20 cm, we recorded which odour stimulus the subjects sniffed first. The video camera automatically split the recordings into 22 min segments. To estimate inter-observer reliability, a second rater coded 23 of 144 (16%) video segments used for statistical analysis, representing all sessions in both groups. Both raters were blind to the location of the odour stimuli. We estimated inter-observer reliability using Spearman's rank correlations for the total durations of each behaviour per individual, box location and session [59]. Where N was smaller than 10, we used the exact version of Spearman's rank correlation (r_s: range=0.346-1, mean±SD=0.733±0.191, see ESM 2 table S3 for detailed results).

f. Statistical Analysis

We conducted all analyses using Linear Mixed Models (LMMs, [60]) with Gaussian error structure and identity link. We set significance at $p<0.05$ and trends at $0.05\leq p<0.1$. We fitted all models in R (version 3.4.0, [61]) using function lmer of R package lme4 (version 1.1-13, [62]).

To test whether chimpanzees react differently to urine odours compared to the control and whether they show a differential behavioural response to ingroup and outgroup odours, we fitted two separate LMMs for each response variable. We used the total duration of behaviours (per subject, odour stimulus and session) as response variables and odour stimulus as test predictor. We included sex, group and age of the subject, session number and box location (for all models) and sex and group of the odour donor and intensity score (for ingroup vs. outgroup models) as control predictors. To account for a potential differential response of males and females towards male and female odours in the ingroup vs. outgroup models, we also included the three-way interaction between odour stimulus, subject sex and odour donor sex. We included subject ID and session ID (for all models) and odour ID (for ingroup vs. outgroup models) as random effects and used a maximal random slopes structure.

To test whether the degree of relatedness influences behavioural responses, we fitted a LMM for each response variable for ingroup odours only. We calculated relatedness coefficients (range = 0-0.5) from pedigree data kindly provided by Leipzig Zoo. We included the relatedness coefficient as test predictor and all control predictors that were significant for the ingroup vs. outgroup models. We included subject ID, odour ID and session ID as random effects and used a maximal random slopes structure (see ESM 2 for details of statistical analyses).

Results

Mode of first investigation

In 83% (73/88) of cases, the first behaviour chimpanzees showed after first approaching a box (apart from looking) was related to olfaction (*sniffing, nose within 20 cm, licking*); in 15% (13/88) of cases, chimpanzees used tactile investigation first, and in 2% (2/88) of cases they only inspected the boxes visually while present within 50 cm (fig. 1). Two adult males (α-male and ex-α-male of group A) never investigated any of the boxes, possibly because they were the oldest males in the group (22 and 40 years) and olfactory function decreases with age [e.g. 63,64]. None of the encounters with the boxes produced any obvious alarm or aggressive responses from the subjects.

First sniffs and number of individuals sniffing

Chimpanzees sniffed more often at outgroup odours first upon their first approach, and this was most apparent in the first two sessions (table 1).

The number of individuals that sniffed a box declined from 20 in the first session to 11 in the last session (table 1). The number of subjects that sniffed all three boxes in a session decreased from 9 individuals in the first session to 1 individual in sessions 4-6 (table 1).

Control vs. odour

Our control vs. odour models revealed a significant influence of the set of predictor variables on the total time individuals spent *sniffing* and *present within 50 cm* of a stimulus, but not of *nose within 20 cm, licking*, or *manipulating* (ESM 2 table S9). More specifically, subjects sniffed odour stimuli and stayed within 50 cm of them for significantly longer than they did for control stimuli (fig. 2, table 2; for detailed results of all predictor variables see ESM 2 table S10). Session number had a highly significant negative effect on the duration of *sniffing* and tended to have a negative effect on *presence within 50 cm* (fig. 3, ESM 2 table S10), indicating habituation over the six sessions. Younger individuals spent significantly more time within 50 cm of the boxes than older individuals (ESM 2 table S10).

Ingroup vs. outgroup

The results of the ingroup vs. outgroup models revealed that the set of predictor variables tended to influence *sniffing* but not *nose within 20 cm, licking, presence within 50 cm* or *manipulating* (ESM 2 table S9). The three-way interaction between odour stimulus, sex of subject ID and sex of odour ID and the three two-way interactions were not significant for *sniffing* (tested by fitting a reduced model without the three-way interaction), so we fitted a reduced model without interactions to obtain interpretable P-values for the main effects. The reduced model revealed a significant effect of odour stimulus, with subjects sniffing outgroup odours longer than ingroup odours (fig. 4, table 2; ESM 2 table S11).

Relatedness

When we tested the effect of relatedness on behavioural responses towards familiar individuals, we found a significant influence of the set of predictor variables on the total durations of *sniffing* and *presence within 50 cm* but not of *nose within 20 cm*, *licking* and *manipulating* (ESM 2 table S9). The total time spent *sniffing* and *present within 50 cm* of familiar odours increased with relatedness to the odour donor (fig. 5, table 2; ESM 2 table S12).

Discussion

We present bioassays testing the effect of conspecific odours on the behaviour of non-human apes. Overall, our results support our predictions, and suggest that chimpanzees are sensitive to social odorants and that they detect group membership and relatedness via olfactory cues.

Control vs. odour and mode of first investigation

Chimpanzees sniffed urine stimuli for significantly longer and stayed within 50 cm of them for longer than they did for the control. This finding suggests that chimpanzees are sensitive to social odorants [65] and reflects responses to urinary stimuli in macaques [66]. However, chimpanzees also showed some interest in and also sniffed the control box, suggesting they use their sense of smell as a general investigation mechanism for novel objects. Supporting this hypothesis, 83% of the first behaviours shown when approaching the boxes for the first time in a session were related to olfaction. Thus, our results highlight the long neglected importance of olfaction in this species.

Ingroup vs. outgroup

Chimpanzees sniffed outgroup urine significantly longer than ingroup urine. Since differences in responsiveness between odorants typically reflect discriminability [5,65], our results suggest that chimpanzees can discriminate between group members and outgroup conspecifics using olfactory cues. Our result is in line with findings for several other mammalian species [e.g. 67–70], including primates. Strepsirrhines [71,72], New World monkeys [13,73] and Old World monkeys [19] discriminate between ingroup and outgroup individuals, responding for longer or more strongly to the scent of familiar than unfamiliar conspecifics. Our findings show that this discrimination mechanism also exists in apes, strengthening existing evidence that the perception of social olfactory signals does not depend on a functional VNO.

Sustained inspection of an unfamiliar outgroup odour may reflect a higher interest in a novel odour or increased efforts to obtain and process new information about the individual scent donor [68]. According to the scent-matching hypothesis, individuals of territorial species learn the scent of marks they encounter in the environment and then compare it with the scent of animals they meet, to facilitate appropriate behaviour [74,75]. Besides obtaining information about the state or identity of an intruder, chimpanzees might also be able to assess the distance to competing groups through the freshness or intensity of the odour or the frequency of outgroup scents encountered [74]. Although chimpanzees are not known to actively scent mark their territory, they sniff and inspect olfactory cues such as urine, faeces or traces of body odour in chimpanzee nests on boundary patrols [44,45]. Our findings suggest that they use these cues to identify the trail of group members and gather information about intruders, and thus to maximize fitness, for example by reducing

aggression.

The ability to discriminate between group members and outgroup individuals via odour may be based on familiarity with or individual recognition of the scent donor. Familiarity alone cannot explain our results, because chimpanzees also detected their degree of relatedness to the urine donor, suggesting that they respond differently based on information encoded in the odour, in addition to familiarity. Whether this information is based on the particular odour donor and thus reflects a mental representation of individual scents in chimpanzees cannot be reliably deciphered based on our findings but opens up an interesting area for future research.

Chemical studies using gas chromatography-mass spectrometry also suggest that chemical cues contain information about group membership in many species (e.g. [76–78]). In primates, chemical profiles reflect group membership in scent gland secretions in mandrills, *Mandrillus sphinx* [20] and body odour in rhesus macaques, *Macaca mulatta* [21]. Given our results it is likely that chimpanzee urinary olfactory profiles also encode information about group membership and kinship [79]. Chemical analyses should investigate the information content (including e.g. sex, age, dominance status, reproductive state) and chemical composition of chimpanzee urine.

Habituation

Our results suggest that chimpanzees habituated to the odour stimuli over the six sessions. Durations of sniffing decreased significantly and the number of animals that sniffed one or more boxes declined considerably, suggesting a loss of interest in the boxes. Future studies of olfactory discrimination abilities in chimpanzees should therefore limit the number of sessions to a maximum of three sessions if three scent stimuli are involved (so that stimulus placement can still be counterbalanced) and rather increase the number of groups tested or apply a habituation-dishabituation paradigm (e.g. [37]).

Many more individuals sniffed outgroup odours first than ingroup or control stimuli in the first two sessions. In the majority of these cases, chimpanzees approached the box containing the outgroup odour straight after entering the inside enclosure, whereas in subsequent sessions they often ignored the boxes on entering the enclosure. They may have quickly realized that there is no real danger of the presence of intruders and thus lost interest in the stimuli. Although the number of first sniffs of outgroup odours was not considerably higher than for ingroup or control stimuli over the six sessions, given our observations in the first two sessions and the strong habituation effect suggesting the first few sessions are most important, we cannot rule out the possibility that chimpanzees perceive important olfactory cues from a greater distance. Further studies of olfactory sensitivity thresholds in chimpanzees are needed to shed more light on their olfactory capabilities.

Relatedness

The more closely related chimpanzees were to a familiar group member, the longer they sniffed and stayed within 50 cm of that individual's urine stimulus. This suggests that chimpanzees can perceive the degree of relatedness through urinary olfactory cues and that such cues may play a crucial role in kin recognition in this species. Our results are in line with a recent study showing that chimpanzees breed with genetically dissimilar mates and take the degree of relatedness into account in their mate choices [56]. Enhanced inspection of familiar kin versus familiar non-kin may reflect generally greater interest in related individuals who are often preferred affiliation and coalition partners [46,53,55,80].

Maternal kin recognition in chimpanzees is well-accepted, and likely based on prior association with the mother [46,52,53,55,80,81]. However, whether chimpanzees can recognise paternal kin is contentious [53,55], although recent evidence that fathers associate more with their offspring than with unrelated infants provides evidence that they can [44, 47]. Recognition of paternal relatives in polygynandrous species likely depends on phenotype matching based on visual, acoustic or olfactory cues [reviewed in 50,82]. Chimpanzees' ability to assess kinship visually through facial recognition is well established [57,58,83]. Our findings suggest that phenotype matching via olfactory cues is a further mechanism for kin recognition in chimpanzees. Our dataset was too small to differentiate between maternal and paternal kin dyads and future studies should investigate whether chimpanzees can use odour to distinguish maternal and paternal kin.

The question of why chimpanzees rely on olfaction when they have a high ability to recognize individuals and kin visually through facial cues is important for our understanding of the evolution of primate communication. Olfactory cues might be especially important when visibility is reduced. Most chimpanzees live in a dense forest habitat where the location and identification of conspecifics that are not close by may depend more on acoustic and odor cues rather than visual cues. Furthermore, chimpanzees sometimes feed, travel and mate at night [46,84–87], and olfaction may help to gather valuable social information in the dark. Finally, since olfactory cues can persist for longer than acoustic and visual cues [88], the ability to recognize individuals via olfaction may be especially important when the sender is no longer present.

Our results contribute to an active area of research on olfactory kin recognition mechanisms. Odour is linked to variation in major histocompatibility complex alleles and plays an important role in kin recognition in many mammalian species, including primates [89,79, reviewed in 90]. Humans, for example, can discriminate between kin and non-kin via olfactory cues alone, and human mothers can recognize the odour of their own offspring [34,35]. Lemurs signal relatedness in their odour profiles [15,91] and detect this information via olfactory cues [16]. We provide the first behavioural evidence

of odour-based kin recognition in apes which is important to prevent infanticide and facilitate inbreeding avoidance and nepotism.

Conclusion

Olfaction in non-human apes has long been neglected. However, humans have retained good olfactory capabilities in the absence of a functional VNO and accessory olfactory bulb. Understanding how these human capabilities have evolved requires the study of the functional significance of odour cues in closely related species, which also lack these anatomical features. Our results provide behavioural evidence that olfaction plays a more important role in chimpanzee social life than hitherto suspected and suggest that chimpanzees obtain information about both inter- and intragroup social relationships from olfactory cues, filling an important gap in our understanding of primate chemical communication and contributing to the argument that a functional VNO is not necessary to perceive olfactory social signals. The ability to obtain information about conspecifics via odour may regulate chimpanzee behaviour and may be an adaptive advantage, for example via conflict management, mate choice, inbreeding avoidance, nepotism or the detection of ovulation. Future studies should investigate the full range of social information contained in ape odour sources using chemical analyses and further bioassays.

Ethics

The study was ethically approved by an internal committee at the Max Planck Institute for Evolutionary Anthropology. Research and animal husbandry comply with the 'EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria', the 'WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums' and the ASAB/ABS 'Guidelines for the Treatment of Animals in Behavioural Research and Teaching'.

Data accessibility

Data are available from the Dryad Digital Repository (doi:10.5061/dryad.0b3k209).

Authors' contributions

SH conceived of, designed and coordinated the study, collected odour samples, conducted the bioassays, carried out the video and statistical analyses and wrote and revised the manuscript.

JMS participated in the conception and design of the study and interpretation of the data and revised the manuscript. Both authors gave final approval for publication.

Competing interests

We declare we have no competing interests.

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Footnotes

Electronic supplementary material is available online at (link to be included).

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Fig. 1 First investigatory behaviours after chimpanzees first approached a box in a test session. Olfactory investigation includes *sniffing*, *nose within 20 cm* and *licking*; tactile investigation includes *touching* and *manipulating*; visual investigation includes just *presence within 50 cm* (paying attention to box without olfactory or tactile investigation)

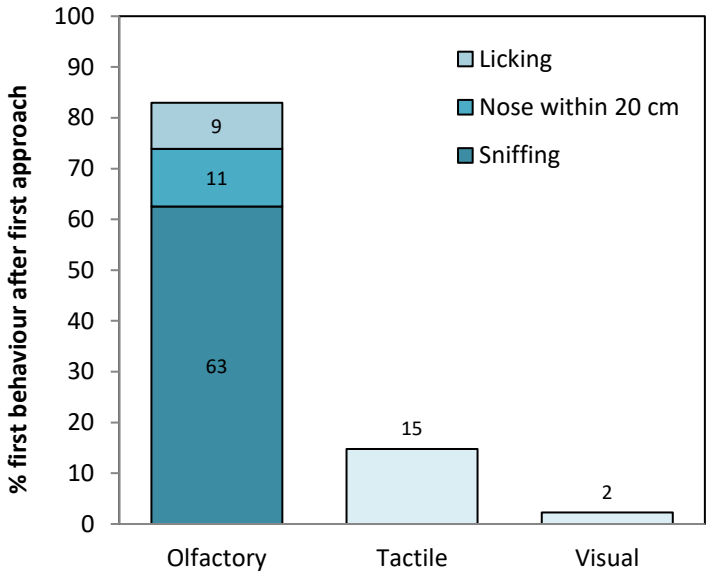

Fig. 2 Total durations of response behaviours towards urine odour samples and an unscented control. Plots show the median (thick horizontal lines) and quartiles (boxes) for *sniffing* and *presence within 50 cm*. Data are presented on a log-scale

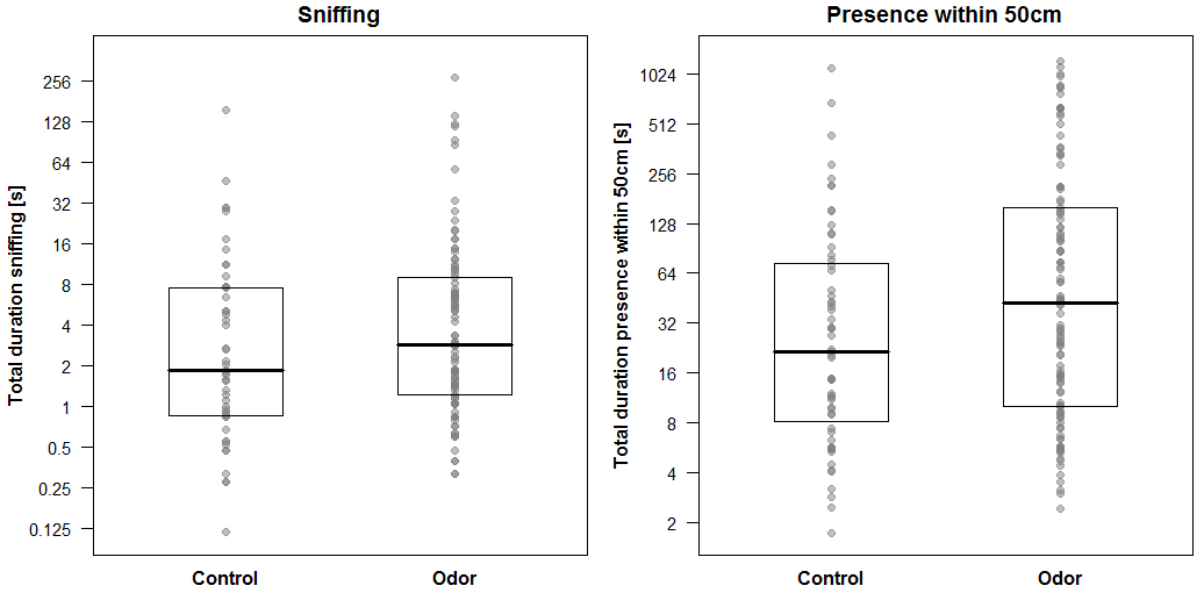

Fig. 3 Effect of session number on the total duration of *sniffing* and *presence within 50 cm*. Dashed lines depict the model (fitted based on all fixed effects manually dummy coded and then centered to a mean of zero), thin dotted lines the 95% confidence intervals of the model. Data are presented on a log-scale

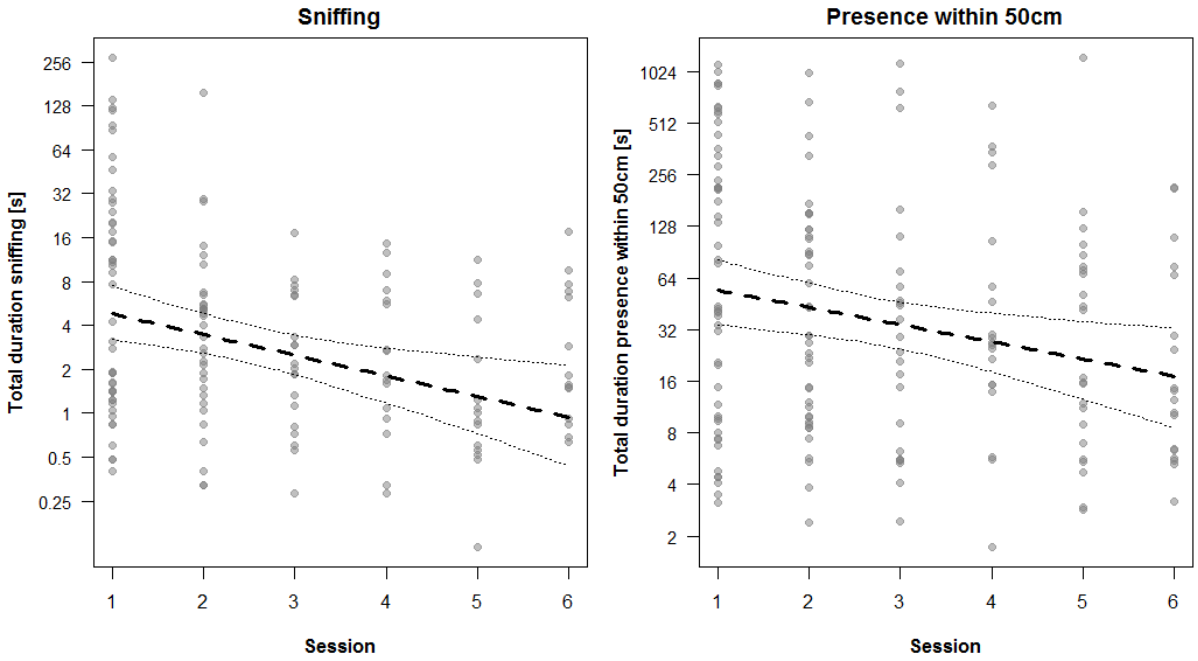

Fig. 4 Total duration of *sniffing* of ingroup and outgroup urine. Plots show the median (thick horizontal lines) and quartiles (boxes). Data are presented on a log-scale

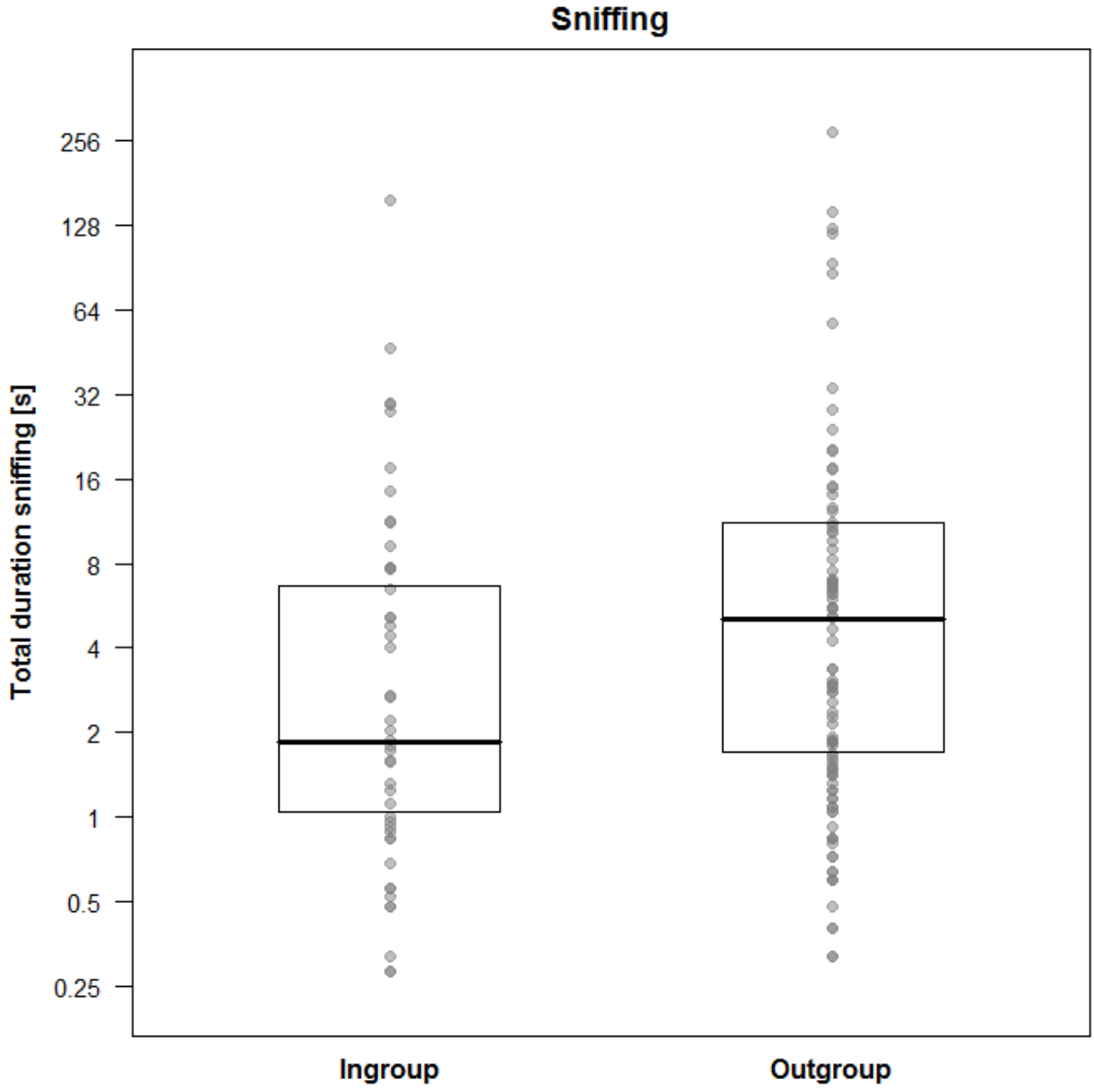

Fig. 5 Effect of relatedness, expressed as the relatedness coefficient, on the total duration of *sniffing* and *presence within 50 cm*. Dashed lines depict the model (fitted based on subject group manually dummy coded and then centered to a mean of zero), thin dotted lines the 95% confidence intervals of the model. Data are presented on a log-scale

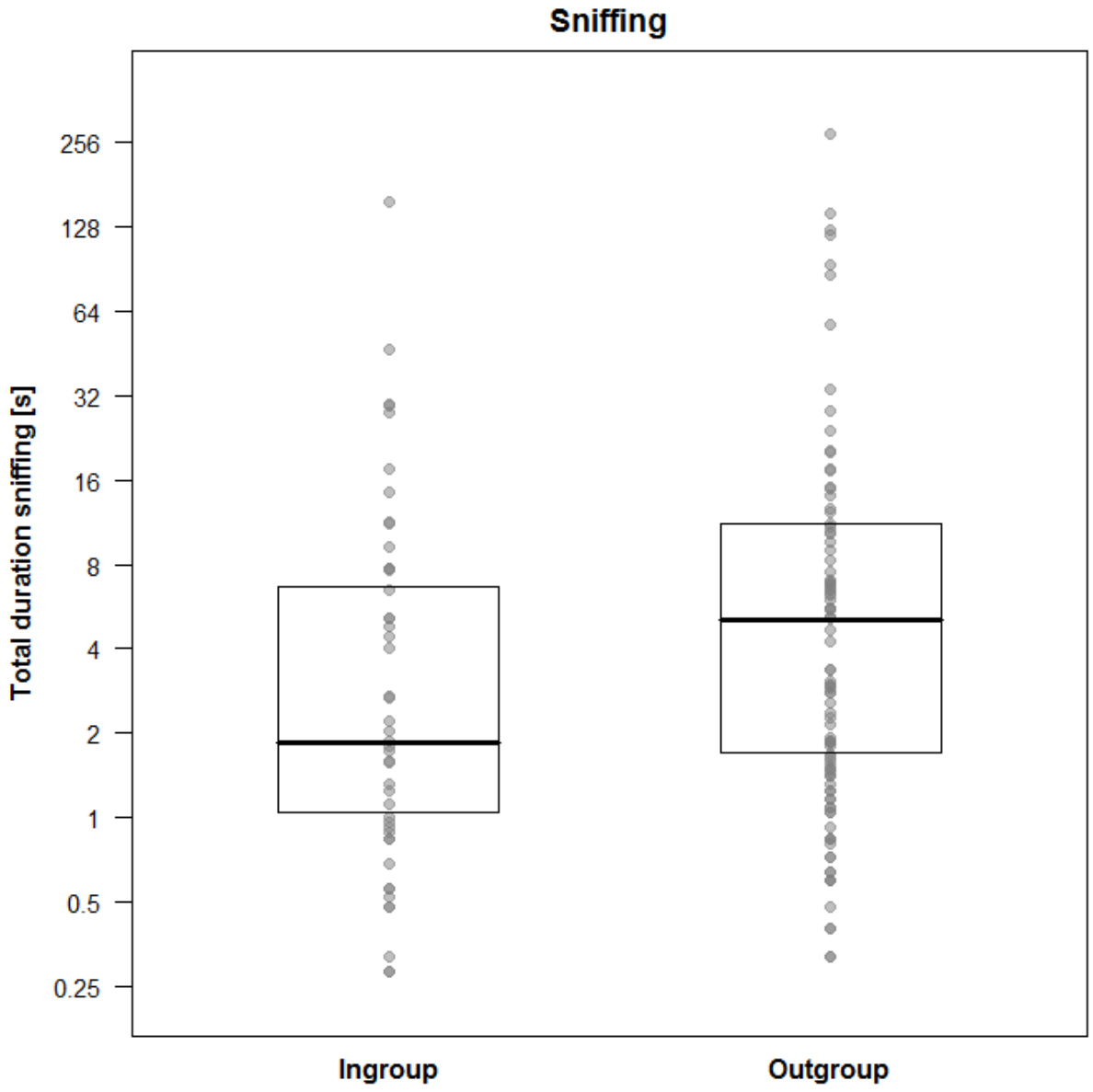

Table 1 Number of individuals that sniffed first at a given odour stimulus and the number of individuals that sniffed all three odours per session

Session		1	2	3	4	5	6	Total observations
Number of individuals that sniffed first at a given odour								
	Outgroup	11	10	2	3	4	2	32
	Ingroup	4	4	7	8	2	4	29
	Control	5	4	2	2	6	5	24
	Total	20	18	11	13	12	11	85
Number of individuals that sniffed all 3 odours								
		9	5	3	1	1	1	20

Table 2 Results of main effects for Linear Mixed Models with Gaussian error structure testing the influence of stimulus type on chimpanzees' response to odour stimuli. For results of control predictors see ESM 2 tables S10-S12. Significances and trends are marked in bold. Ref = reference level. Colons represent the interaction between fixed effects

Model	Response variable	Predictor variable	Estimate	SE	χ^2	p
Control vs. odour	Sniffing	Odour (ref = control)	0.482	0.213	4.660	**0.031**
	Nose within 20cm	Odour (ref = control)	0.362	0.243	1.913	0.167
	Licking	Odour (ref = control)	0.382	0.293	1.572	0.210
	Presence within 50cm	Odour (ref = control)	0.507	0.234	3.961	**0.047**
	Manipulating	Odour (ref = control)	0.393	0.274	1.985	0.159
Ingroup vs. outgroup	Sniffing	Odour (ref = ingroup)	0.564	0.251	4.675	**0.031**
	Nose within 20 cm	Odour:Subject sex:Odour sex	-0.820	1.246	0.423	0.515
	Licking	Odour:Subject sex	-0.222	0.769	0.101	0.751
		Odour:Odour sex	-0.560	0.851	0.419	0.517
	Presence within 50 cm	Odour:Subject sex:Odour sex	-2.718	1.413	2.975	**0.085**
	Manipulating	Odour:Subject sex	1.605	0.735	3.981	**0.046**
		Odour:Odour sex	0.032	0.886	0.001	0.972
Relatedness	Sniffing	$r^{(2)}$	0.544	0.226	5.152	**0.023**
	Nose within 20cm	$r^{(2)}$	1.839	1.506	1.461	0.227
	Licking	$r^{(2)}$	0.316	0.351	0.762	0.383
	Presence within 50cm	$r^{(2)}$	0.791	0.246	8.719	**0.003**
	Manipulating	$r^{(2)}$:Subject sex	0.429	0.414	1.040	0.308

(1): not shown because lacks a reasonable interpretation

(2): z-transformed to mean=0 and sd=1; mean and sd of the original variables are presented in ESM 2 table S13